Increased anthropogenic disturbance and aridity reduce phylogenetic and functional diversity of ant communities in Caatinga dry forest

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HIGHLIGHTS

- Ant biodiversity patterns under global change drivers are assessed in Caatinga.
- Functional and phylogenetic diversity decrease with aridity and human disturbances.
- Human disturbance and aridity interact in complex ways to endanger biodiversity.
- Aridity can intensify the negative effects of disturbance on biodiversity.
- Concerns about the future of biodiversity in neotropical semi-arid regions.

GRAPHICAL ABSTRACT
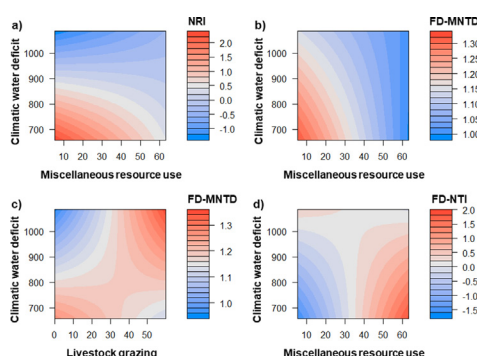
ABSTRACT

Anthropogenic disturbance and climate change are major threats to biodiversity. The Brazilian Caatinga is the world's largest and most diverse type of seasonally dry tropical forest. It is also one of the most threatened, but remains poorly studied. Here, we analyzed the individual and combined effects of anthropogenic disturbance (three types: livestock grazing, wood extraction, and miscellaneous use of forest resources) and increasing aridity on taxonomic, phylogenetic and functional ant diversity in the Caatinga. We found no aridity and disturbance effects on taxonomic diversity. In spite of this, functional diversity, and to a lesser extent phylogenetic diversity, decreased with increased levels of disturbance and aridity. These effects depended on disturbance type: livestock grazing and miscellaneous resource use, but not wood extraction, deterministically filtered both components of diversity. Interestingly, disturbance and aridity interacted to shape biodiversity responses. While aridity sometimes intensified the negative effects of disturbance, the greatest declines in biodiversity were in the wettest areas. Our results imply that anthropogenic disturbance and aridity interact in complex ways to endanger biodiversity in seasonally dry tropical forests. Given global climate change, neotropical semi-arid areas are habitats of concern, and our findings suggest Caatinga conservation policies must prioritize protection of the wettest areas, where biodiversity loss stands to be the greatest. Given the major ecological relevance of ants, declines in both ant phylogenetic and functional diversity might have downstream effects on ecosystem processes, insect populations, and plant populations.

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1. Introduction

Anthropogenic disturbance and global climate change are key threats to biodiversity (Bellard et al., 2012) because they have significant impacts on biological populations and community organization. This is especially true in seasonally dry tropical forests (SDTFs), which are experiencing increased rates of both acute and chronic disturbance. Major acute disturbances include habitat loss and fragmentation (Miles et al., 2006). Major chronic disturbances (hereafter referred to as CADs—chronic anthropogenic disturbances [sensu Singh, 1998]) include livestock grazing, wood extraction, and the exploitation of miscellaneous forest resources. These activities all result in the removal of significant amounts of biomass. In STDFs, few efforts have been made to understand the impacts of CADs on biodiversity, but negative impacts have been described in communities of both plants (Sagar et al., 2003; Ribeiro et al., 2015, 2016; Rito et al., 2017) and animals (Ribeiro-Neto et al., 2016; Oliveira et al., 2017). Climate change also threatens SDTFs (Dirzo et al., 2011) and might even exacerbate the effects of anthropogenic disturbances (Hirota et al., 2011; Ponce-Reyes et al., 2013; Gibb et al., 2015a; Frishkoff et al., 2016). Hot and arid environments are likely at the greatest risk (Anderson-Teixeira et al., 2013; Gibb et al., 2015a).

Studies of biological communities have generally focused on patterns of species diversity, which are often quantified using species richness and/or composition (Pavoine and Bonsall, 2011). However, new diversity metrics that incorporate information about phylogenetic diversity (PD) and functional diversity (FD) can reveal more information about community organization in different contexts (Faith, 1992; Webb et al., 2002; Petchey and Gaston, 2006; Swenson, 2014), including those marked by anthropogenic disturbance and climate change (Mouillot et al., 2013). While phylogenetic diversity reflects the accumulated evolutionary history of a community (Webb et al., 2002), functional diversity reflects the diversity of morphological, physiological, and ecological traits found therein (Petchey and Gaston, 2006). It is generally accepted that PD and FD can increase with taxonomic diversity by chance, since the presence of more species should mean that more lineages and functions are represented. However, these relationships are not always linear. Two communities with equal taxonomic diversity might greatly differ in PD and FD (Petchey and Gaston, 2006; Safi et al., 2011; Arnan et al., 2015, 2017) due to different levels of functional redundancy, different evolutionary histories, and/or contrasting environmental conditions. However, a strong correlation between FD and PD would be expected if the functional traits that allow species to persist in the environment are evolutionarily conserved, that is to say, they display phylogenetic signals (Webb et al., 2002; Cavender-Bares et al., 2009). Remarkably, very little is known about how PD and the functional composition of animal communities change in response to disturbance and environmental conditions, especially in SDTFs.

When examining biodiversity patterns, ants are a good study group —they are among the most diverse and abundant terrestrial organisms on earth and they are highly sensitive to environmental change (Hölldobler and Wilson, 1990). Moreover, ants play an important role in many basic ecosystem services (Bihn et al., 2010, Del Toro et al., 2012). In particular, ants are crucial contributors to soil cycling and aeration, organic matter decomposition, seed dispersal, and plant protection (Del Toro et al., 2012). Ants are extremely phylogenetically diverse, especially in the tropics (Hölldobler and Wilson, 1990), and ant morphological traits have frequently been used to infer ecosystem services (Weiser and Kaspari, 2006; Gibb et al., 2015b; Parr et al., 2017; Salas-López, 2017).

In this study, we analyzed the effects of CADs and climate change, notably increasing aridity, on the phylogenetic and functional diversity of ants in the Brazilian Caatinga, the largest and most diverse of the world's SDTFs (Leal et al., 2005). The Caatinga is the third most-threatened Brazilian ecosystem and yet is the most poorly studied and understood (Overbeck et al., 2015; Oliveira and Bernard, 2017). The 27 million people living in the Caatinga are highly dependent on its natural resources for their livelihoods, which has resulted in its slow degradation over time (Leal et al., 2005; Ribeiro et al., 2015). Moreover, the Caatinga is one of the six ecosystems with the greatest intrinsic vulnerability to climate variability (Seddon et al., 2016); climate models consistently predict a reduction in rainfall levels (22%) and an increase in temperature (3–6 °C) (Magrin et al., 2014).

In this context, the Caatinga is a good model system with which to investigate the effects of anthropogenic disturbance and climate change (i.e., increased aridity) on the biological communities of dry forests. It can also be used to characterize changes in community organization arising from transformations in SDTFs. Previous studies in the Caatinga found no or small differences in ant species richness along CAD gradients; however, large changes in species composition were observed (Ribeiro-Neto et al., 2016; Oliveira et al., 2017). This finding suggests shifts in phylogenetic and functional diversity along CAD gradients. We therefore first corroborated that species diversity is not modulated by CAD and aridity gradients, and hypothesize the following: (a) PD and FD will decrease as anthropogenic disturbance and aridity increase; (b) PD and FD will decrease even more sharply in areas that are both highly disturbed and arid; and (c) PD and FD patterns along gradients of disturbance and aridity will be driven by deterministic processes rather than by stochasticity.

2. Materials and methods

2.1. Study area

This study was conducted in Catimbau National Park (8°24′00″ and 8°36′35″ S; 37°0′30″ and 37°1′40″ W, state of Pernambuco, Brazil), which cover an area of 607 km² of Caatinga vegetation (Sociedade Nordestina de Ecologia, 2002). The climate is hot. Mean annual temperature is 25 °C, and mean annual rainfall ranges between 1100 mm in the southeast to 480 mm in the northwest (Rito et al., 2017). However, the park experiences substantial interannual and spatial variability in conditions (Sociedade Nordestina de Ecologia, 2002). Most of the park has quartzolic sandy soils (70%), but planosols (15%) and lithosols (15%) are also present (Sociedade Nordestina de Ecologia, 2002). The dominant families of woody plants are Fabaceae, Euphorbiaceae, and Boraginaceae; on the surface of the forest floor, Cactaceae, Bromeliaceae, Malvaceae, Asteraceae, and Fabaceae dominate (Rito et al., 2017).

The park was established in 2002 (Sociedade Nordestina de Ecologia, 2002), but its original human inhabitants remain; they continue to hunt, graze livestock, extract timber, collect firewood, and harvest other plant resources (Rito et al., 2017). Their historical presence has resulted in an extensive mosaic of differential land use and anthropogenic pressure on biota. This fact means Catimbau represents an excellent opportunity for examining how anthropogenic disturbance (e.g., farming, livestock grazing, extraction of timber, firewood gathering, and hunting) affects the biota of the Caatinga. Also, the considerable variation in precipitation within the park (100%) can help reveal whether high levels of aridity can intensify the negative effects of human disturbance.

2.2. Characterization of disturbance and aridity gradients

We sampled 20 0.1-ha plots (20 × 50 m; separated by at least 2 km) located within areas dominated by old-growth vegetation; the plots occurred along an aridity gradient and experienced varying degrees of CAD (Fig. 1). Thanks to aerial photographs and preliminary interviews with locals, we could confirm that the plots had not experienced any acute disturbances over the past 80 years. All plots were located in areas with the same soil type (sandy soil), slope (flat terrain), and vegetation type (dry forest with short-stature trees) (Rito et al., 2017).

We characterized disturbance intensity by calculating three different indices that corresponded to the main CADs affecting the Caatinga in general and Catimbau in particular: (1) livestock grazing (LG)—consumption of vegetation, trampling, and other physical damage caused by cattle and goats; (2) wood extraction (WE)—the extraction of dead and live wood for fuel, fence construction, and artisanal production; and (3) miscellaneous resource use (MU)—use of non-wood resources by humans (e.g., food and medicinal plants, hunting). Index values were calculated using the following formula: $I = \frac{\sum_{i=1}^{n} (y_i - y_{min})/(y_{max} - y_{min})}{n} \times 100$, where I is disturbance intensity; y_i is the observed value for a given disturbance metric in plot i; y_{min} is the minimum observed value for the disturbance metric across all plots; y_{max} is the maximum observed value for the disturbance metric across all plots; and n is the number of individual disturbance metrics incorporated in the index. This formula thus standardizes the metrics (sometimes of different units) to take on a value between 0 and 1, allowing them to be combined in the same index. Index values ranged from 0 to 100 (from no disturbance to maximum-intensity disturbance). Both the LG and WE indices quantified disturbances that were directly measured in the field. For the LG index, we estimated grazing levels by measuring the length of goat trails and the frequency of cattle and goat dung (see Appendix S1 for details). Then, we combined the two estimates of goat grazing (trail length and dung frequency) by means of principal component analysis (PCA). Both measures were highly positively correlated ($r > 0.90$) with the first PCA axis, which explained 88% of variance. We therefore used its coordinates to obtain a single measure of goat grazing. The LG index was then calculated by inputting measures of goat grazing and cattle dung frequency into the formula above. For the WE index, we estimated the extraction of live wood and the collection of firewood (Appendix S1) and plugged them directly into the formula above. Finally, the MU index was determined using three indirect variables that are proxies for local anthropogenic pressure and habitat accessibility. More specifically, we estimated two relevant geographic distances—plot proximity to the nearest house and plot proximity to the nearest road (using satellite imagery and ArcGis 10.1 software). We also used a socioecological variable—the number of people living in the area that influence the plot (Appendix S1). Then, the values of these metrics were inputted into the formula above to obtain the MU index. The three disturbance indices displayed a wide range of values (min-max for LG: 0–60, WE: 0–100, and MU: 5–63; Fig. 1 and Appendix S2) and were not highly correlated (LG vs. WE: $r = 0.05$, LG vs. MU: $r = 0.61$, and MU vs. WE: $r = -0.10$). This result underscores that the indices are quite independent and measure different forms of anthropogenic disturbance.

Field-based research into temporal evolutionary change typically requires long-term data that are unavailable for most systems.
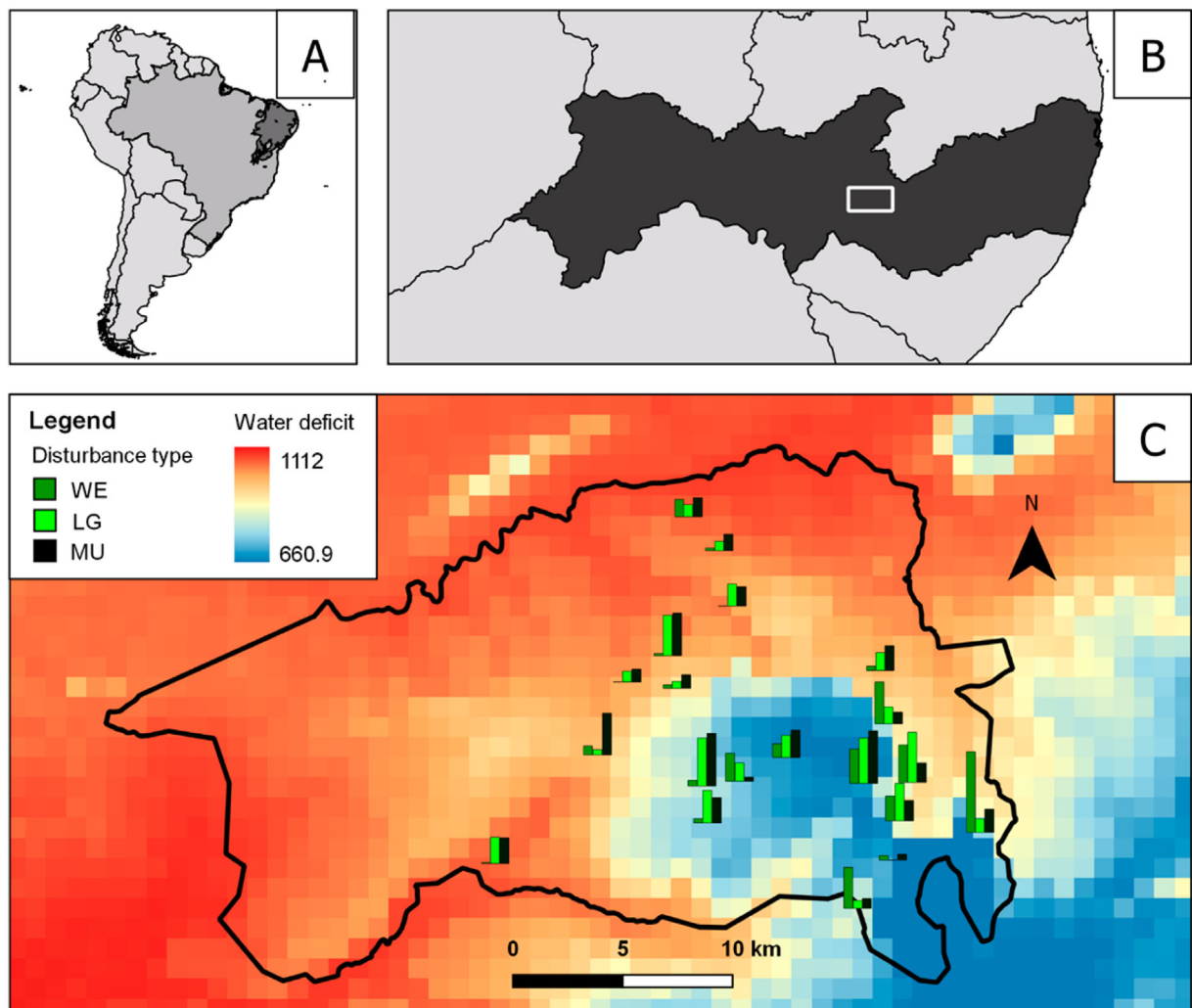

Fig. 1. Location of the study region (in dark gray; within Brazil) (A), Catimbau National Park (white box; within Pernambuco) (B), and the study plots (bar graphs; within Catimbau) (C). The bar graphs depict the intensity of each anthropogenic disturbance (wood extraction, WE; livestock grazing, LG; miscellaneous resource use, MU) on each plot. The color scale depicts aridity (i.e., climatic water deficit).

Furthermore, carrying out climate change studies in the laboratory is difficult, especially if the aim is to address issues at the community level. At present, the only effective means of exploring changes in biodiversity due to rapid climatic shifts is the space-for-time approach, where space acts as a substitute for time (Blois et al., 2013). However, historical and evolutionary processes might not act similarly along temporal versus spatial gradients. Consequently, inferences based on certain climatic conditions can, but do not always, reflect the responses expected over the timeline of future climate change (Bellard et al., 2012). Here, we explored the potential effects of declining precipitation and increasing temperature in the Caatinga by analyzing changes in aridity along a spatial gradient. Aridity was estimated using mean annual climatic water deficit, which is the difference between potential evapotranspiration (PET) and actual evapotranspiration (AET; based on biologically usable energy and water) (Lutz et al., 2010). Climatic water deficit was calculated using 30-arc-second (1-km) resolution maps of long-term mean annual PET and AET (CGIAR-CSI's Global Aridity and PET Database and Global High-Resolution Soil-Water Balance Database; www.csi.cgiar.org/([2009])). These maps were generated using temperature and precipitation data from the WorldClim global climate data repository (www.worldclim.org). For each plot, the difference between annual PET and AET was calculated to obtain a climatic water deficit value. All calculations were performed using ArcGIS 10.1 software. Climatic water deficit values ranged from 658 mm (minimum aridity) to 1086 mm (maximum aridity), and was not correlated to any of the disturbance indices ($r = -0.14$, -0.18 and -0.06 for LG, WE and MU, respectively).

2.3. Sampling ant communities

Each plot contained 20 pitfall traps (4×5 grid; separated by 5 m). The traps were 4.5-cm diameter plastic containers partially filled with a mixture of alcohol, ethylene glycol, and soap. Traps were left open for a single 48-h period in March 2015, at the beginning of the rainy season. All the ants collected were sorted to morphospecies following Baccaro et al. (2015). They were identified when possible; unidentifiable species were assigned a code. Identifications were verified by R. Feitosa (Laboratório de Sistemática e Biologia de Formigas, Universidade Federal do Paraná). Vouchers of all species are available at the Universidade Federal Pernambuco in Recife and the Universidade Federal do Paraná in Curitiba.

2.4. Characterization of ant phylogenetic relationships

At present, there is no complete, species-level ant phylogeny. We therefore used an approach that incorporated as much information as possible given our current understanding of ant relationships while simultaneously accounting for existing phylogenetic uncertainty. We began by using a backbone tree derived from a time-calibrated, genus-level phylogeny (Moreau and Bell, 2013); however, the phylogenetic relationships within Myrmicinae were taken from Ward et al. (2015). This phylogeny was then pruned to keep a single species per genus and thus generate a genus-level phylogeny. We subsequently used the list of species in our dataset (Appendix S3) to simulate 1000 species-level phylogenies. Species relationships within genera were obtained from a Yule (pure-birth) process using the *genus.to.species.tree* function in the phytools package (Revell, 2012) in R (R Development Core Team, 2016). However, given that one genus (*Mycetophylax*) was missing, we randomly added this lineage to our genus-level tree as a sister genus of *Kalathomyrmex* (Klingenberg and Brandão, 2009) prior to the addition of species in each iteration. The entire process was repeated 1000 times to account for phylogenetic uncertainty in later analyses.

2.5. Characterization of ant functional traits

We quantified functional diversity using a suite of morphological traits that reflect body size, foraging capacity, foraging period, and resource acquisition mode (Bihn et al., 2010; Parr et al., 2017). These traits serve as proxies for the impact a species might have on ecosystem processes related to resource use. By focusing on morphological traits, we obviously ignored some aspects of the ants' ecology; however, direct links between morphological traits and functional roles have been observed in ants (Table 1). For each ant species, we determined body size (Weber's length), relative eye length, relative scape length, relative mandible length, relative clypeus length, and relative leg length (Table 1). We standardized all trait measurements (except Weber's length) by dividing each by the Weber's length to limit correlations with body size. The trait values were then log-transformed to achieve normality. We measured approximately six randomly selected workers, and the mean measurements were used as the species-specific values for monomorphic and polymorphic species. In species with distinct minor and major worker castes, only minor workers were employed. In total, 503 workers representing 69 ground-foraging ant species were measured (number of individuals measured per species: mean $\pm$ SE = 7.4 $\pm$ 0.16, median = 6.4, min = 1 and max = 70).

2.6. Estimating taxonomic, phylogenetic and functional diversity

For each plot, taxonomic diversity was characterized as species richness (S, the number of ant species in each plot) and species diversity (Shannon diversity index, H, which accounts for both species richness and evenness).

We measured five complementary metrics of phylogenetic diversity and functional diversity (Swenson, 2014). Phylogenetic diversity was

Table 1
Morphometric traits of workers used to characterize the functional diversity of Caatinga ant communities (Catimbau National Park, Pernambuco state, NE Brazil).

Trait	Functional significance	Reference	Definition
Body size (Weber's length)	Strongly correlated with many physiological, ecological, and life-history traits, including resource use	Kaspari and Weiser, 1999, Bihn et al., 2010	Maximum longitudinal length from the most anterior part of the clypeus to the occipital margin, in full face view
Relative eye length	Likely correlated with main foraging period (day vs. night)	Bihn et al., 2010	Ratio of eye length to mesosoma length
Relative scape length	Possibly correlated with ability to receive chemosensory information. Ants with long scapes may be more sensitive to pheromone trails.	Weiser and Kaspari, 2006	Ratio of scape length to mesosoma length
Relative mandible length	Possible indicator of predatory lifestyle and thus types of resources consumed	Weiser and Kaspari, 2006	Ratio of mandible length to mesosoma length
Relative clypeus length	Correlated with sucking ability and liquid-feeding behavior	Davidson et al., 2004	Ratio of clypeus length to mesosoma length
Relative leg length	Possibly correlated with resource acquisition mode and foraging efficiency, as well as with the ability to cope with the foraging surface temperature	Kaspari and Weiser, 1999, Bihn et al., 2010	Ratio of leg length (combined length of femur and tibia) to mesosoma length

estimated using the following indices (Table 2): (a) Faith's phylogenetic diversity (Faith's PD); (b) mean pairwise distance (MPD); (c) mean nearest-taxon distance (MNTD); (d) the net relatedness index (NRI); and (e) the nearest taxon index (NTI). Faith's PD is widely used in conservation research (Forest et al., 2007; Morlon et al., 2011) and, here, was the total branch length (divergence time) of the phylogenetic tree linking all the species represented in the community (Faith, 1992). MPD was the mean distance (in millions of years) between two randomly selected individuals within a specific plot (considering conspecifics), while MNTD was the mean distance separating each individual in the community from its closest heterospecific relative (Webb et al., 2002). Thus, when MNTD is more strongly correlated with environmental gradients than is MPD, it indicates that the environment has a stronger effect on terminal than basal community phylogenetic composition. Since both metrics might depend on species richness, we also measured the standardized effect size (SES) for MPD and MNTD (i.e., NRI and NTI, respectively) by comparing observed phylogenetic relatedness to expected phylogenetic relatedness in null communities generated at random. Random communities were generated by randomizing the community data matrix using the independent swap algorithm 1000 times. Then, we computed the SES of MPD and the SES of MNTD by taking the difference between the mean phylogenetic distances in the observed communities versus in the null communities, standardized by the standard deviation of the phylogenetic distances in the null data ($SES = (mean_{obs} - mean_{null})/sd_{null}$) (Webb et al., 2002; Swenson, 2014). We then multiplied the SES of MPD and the SES of MNTD by −1, obtaining NRI and NTI, respectively. The NRI and NTI values indicated whether taxa in the community were more closely related (positive values) or less closely related (negative values) than expected by chance. However, the two indices differ in phylogenetic scale. NRI reflects information about whole phylogenies, while NTI reflects information about branch tips.

The phylogenetic indices were calculated using the *pd.* (PD), *ses.mpd* (MPD and NRI), and *ses.mntd* (MNTD and NTI) functions in the picante package in R. For each index, 1000 phylogenetic trees were simulated, and the mean value was retained for use in further analyses.

To characterize functional diversity, we calculated Petchey and Gaston's FD (hereafter PG-FD; Petchey and Gaston, 2002), as well as the functional equivalents of MPD, MNTD, NRI, and NTI (hereafter, FD-MPD, FD-MNTD, FD-NRI, and FD-NTI) (Table 2). PG-FD is the total branch length of the functional dendrogram that results when species

are clustered in trait space (Petchey and Gaston, 2002). Here, the functional dendrogram was created by generating a Euclidean distance matrix from the z-standardized trait values of the different species and by clustering the species using the unweighted pair group method with arithmetic mean (UPGMA). PG-FD was calculated using the *alpha* function in the BAT package in R. FD-MPD, FD-NRI, FD-MNTD, and FD-NTI were calculated as described above, except that trait-based Euclidean distances rather than phylogenetic distances (i.e., divergence times) were used. Note that while Faith's PD and PG-FD are not abundance-weighted indices, all the remaining indices are abundance-weighted, i.e. they reflect trends in both abundance and evenness.

2.7. Statistical analyses

We used general linear models (GLMs) with a Gaussian distribution error and "identity" link to analyze the relationships between the taxonomic, phylogenetic and functional diversity indices and the disturbance and aridity gradients. We used a separate model for each response variable (S, H, Faith's PD, MPD, MNTD, NRI, NTI, PG-FD, FD-MPD, FD-MNTD, FD-NRI, and FD-NTI); the explanatory variables were climatic water deficit, the LG index, the WE index, and the MU index. Interactions between the disturbance indices and water deficit were also included. We employed Akaike's information criterion with a correction for finite sample sizes (AICc) to select the best-supported models; this approach reduces the problems associated with multiple testing, colinearity of explanatory variables, and small sample sizes (Burnham and Anderson, 2002). All the initial models were full models. The best-supported models were selected based on their AICc weights, which reveal the relative likelihood of a given model—based on the data and the fit—scaled to one; thus, models with a delta (AICc difference) of <2 were selected (Burnham and Anderson, 2002). The relevant variables were those that were retained in the best-supported models (except, obviously, when the best-supported model consisted only of the intercept). Model selection was carried out using the *dredge* function in the MuMIn package in R.

2.8. Phylogenetic signals in ant functional traits

To test for phylogenetic signals (i.e., the degree of phylogenetic constraint in species resemblance) in the six morphological traits, we computed Pagel's λ (Pagel, 1999). This index compares the observed

Table 2
List of selected phylogenetic and functional diversity metrics, their description and references, and their range of values in this study.

Diversity metric	Description	Reference	Range
Phylogenetic diversity			
Faith's PD	Total branch length (divergence time) of the phylogenetic tree linking all the species represented in the community. Not abundance-weighted.	Faith, 1992	770.9–1234.0
Mean pairwise distance (MPD)	Mean phylogenetic distance (in millions of years) between two randomly selected individuals within a specific plot (considering conspecifics). Abundance-weighted.	Webb et al., 2002, Swenson, 2014	143.1–177.0
Mean nearest-taxon distance (MNTD)	Mean phylogenetic distance (in millions of years) separating each individual in the community from its closest heterospecific relative. Abundance-weighted.	Webb et al., 2002, Swenson, 2014	58.43–120.88
Net relatedness (NRI)	Quantifies the structure of a sample phylogeny derived from the mean phylogenetic distance, consequently capturing the degree of clustering of the phylogeny from root to terminal leaves. Abundance-weighted.	Webb et al., 2002, Swenson, 2014	−1.63–2.82
Nearest taxon index (NTI)	Quantifies the terminal structure of the sample phylogeny, hence only captures the clustering of the terminal nodes in the tree. Abundance-weighted.	Webb et al., 2002, Swenson, 2014	−1.50–1.33
Functional diversity			
Petchey and Gaston's FD	Total branch length of the functional dendrogram that results when species are clustered in trait space. Not abundance-weighted.	Petchey and Gaston, 2002	21.28–34.28
FD-MPD (MPD with functional data)	Mean functional distance between two randomly selected individuals within a specific plot (considering conspecifics). Abundance weighted.	Webb et al., 2002, Swenson, 2014	2.23–2.77
FD-MNTD (MNTD with functional data)	Mean functional distance separating each individual in the community from its closest co-occurring relative. Abundance weighted.	Webb et al., 2002, Swenson, 2014	0.92–1.37
FD-NRI (NRI with functional data)	Quantifies the structure of a sample functional dendrogram derived from the mean functional distance, consequently capturing the degree of clustering of the functional dendrogram from root to terminal leaves. Abundance weighted.	Webb et al., 2002, Swenson, 2014	−1.42–1.66
FD-NTI (NTI with functional data)	Quantifies the terminal structure of the sample functional dendrogram, hence only captures the clustering of the terminal nodes in the functional dendrogram. Abundance weighted.	Webb et al., 2002, Swenson, 2014	−1.73–1.62

distribution of traits with the expected distribution of traits based on a Brownian motion model of evolution. Values of 0 and 1 indicate the absence and presence, respectively, of a phylogenetic signal under such conditions. We computed λ values for each trait and for each of the 1000 simulated trees using the *phylosig* function in the phytools package (Revell, 2012) in R. To conservatively test signal significance, we used a likelihood ratio test based on the minimum values to estimate the probability that the observed λ differed from the null λ value of 0. It is important to note that, given that the simulated tree might lead to an underestimation of phylogenetic signal, our estimates of lambda are probably conservative.

3. Results

3.1. Ant communities

Our traps captured representatives of 71 ant species belonging to 23 genera and 7 subfamilies (Appendix S4). Myrmicinae was by far the most species-rich subfamily (39 species), followed by Dolichoderinae and Formicinae (12 and 9 species, respectively). The most species-rich genus was *Pheidole* (14 species), followed by *Dorymyrmex* (9 species) and *Solenopsis* (8 species); *Camponotus*, *Cephalotes*, and *Pseudomyrmex* were represented by 6 species each. The most frequently occurring species were *Ectatomma muticum* (61.1% of all traps), *Solenopsis virulens* (44.8% of all traps), and *Dinoponera quadriceps* (41.2% of all traps). *Dinoponera quadriceps* occurred on all 20 plots, while *Ectatomma muticum* and *Solenopsis virulens* occurred on 19 plots. Nineteen and 18 species occurred on one and two plots, respectively. We found between 15 and 26 species per plot. Species richness and species diversity were not modulated by the aridity and disturbance gradients (Appendix S5).

3.2. Phylogenetic and functional diversity along disturbance and aridity gradients

The best-supported models retained climatic water deficit (called aridity hereafter), the LG index, and the MU index, but not the WE index (Table 3, Appendix S5). Faith's PD decreased along the LG gradient (Table 3, Fig. 2a, $R^2 = 0.31$). The NRI decreased along the aridity, LG (Fig. 2b, $R^2 = 0.02$), and MU gradients (Table 3): communities transitioned from being more closely related to less closely related. This result indicates that ants coexisting under the same aridity or disturbance conditions are non-randomly phylogenetically clustered. Furthermore, the NRI was influenced by an interaction between aridity and MU (Fig. 3a, $R^2 = 0.64$). More specifically, the decrease in the NRI along the aridity gradient was much stronger in areas with lower MU, and the negative relationship between the NRI and MU became positive when aridity was greater. None of the variables considered here helped explain MPD, MNTD, or NTI values.

PG-FD decreased as aridity and LG increased (Table 3, Fig. 2c,d, $R^2 = 0.11$ and $R^2 = 0.22$, respectively). FD-MPD decreased along the aridity gradient (Table 3, Fig. 2e, $R^2 = 0.16$). The FD-NRI was not associated with any of the explanatory variables (Table 3). FD-MNTD generally decreased along the aridity, LG, and MU gradients (Table 3), but there were also complex aridity-by-disturbance interactions. More specifically, when aridity was lower, FD-MNTD increased faster as MU declined, and FD-MNTD only decreased along the aridity gradient when MU was lower (Fig. 3b, $R^2 = 0.20$). At the same time, FD-MNTD decreased and increased with LG at low and high levels of aridity, respectively. It also increased and decreased with aridity at low and high levels of LG (Fig. 3c, $R^2 = 0.22$), respectively. The FD-NTI generally increased along the aridity and MU gradients (Table 3), meaning that communities transitioned from being functionally overdispersed to functionally clustered. However, there was once again an interaction between aridity and disturbance. The positive relationship between disturbance and the FD-NTI became negative in the most arid areas, and the positive relationship between aridity and the FD-NTI became negative in the most disturbed areas (Table 3, Fig. 3d, $R^2 = 0.56$).

3.3. Phylogenetic signals in ant functional traits

Strong, significant ($p < 0.0001$) phylogenetic signals were present in all traits, indicating that they were phylogenetically conserved. The only exception was relative clypeus length ($p = 0.334$) (Appendix S6).

4. Discussion

Our results highlight how ant phylogenetic diversity and functional diversity changed, despite unmodified taxonomic diversity, along CAD and aridity gradients in the Caatinga, a type of SDTF found exclusively in Brazil. In the 21st century, increased CAD and aridity are the main threats faced by biota in dry tropical regions (Dirzo et al., 2011). Overall, we found that functional diversity and, to a lesser extent, phylogenetic diversity, decreased with increasing aridity. Both types of diversity also decreased as anthropogenic disturbance increased; livestock grazing and miscellaneous resource use had an influence while wood extraction did not. Remarkably, we also found that anthropogenic disturbance and aridity interacted to shape biodiversity responses. We discovered clear evidence that the main mechanism involved was habitat filtering.

We found support for our first hypothesis: in general, increased levels of disturbance and aridity decreased ant phylogenetic diversity and functional diversity. However, these relationships were somewhat complex because different patterns were observed in different diversity metrics. Also, environmental gradients interacted in different ways. The patterns were especially complex in the case of phylogenetic diversity. For example, increased levels of livestock grazing reduced the amount
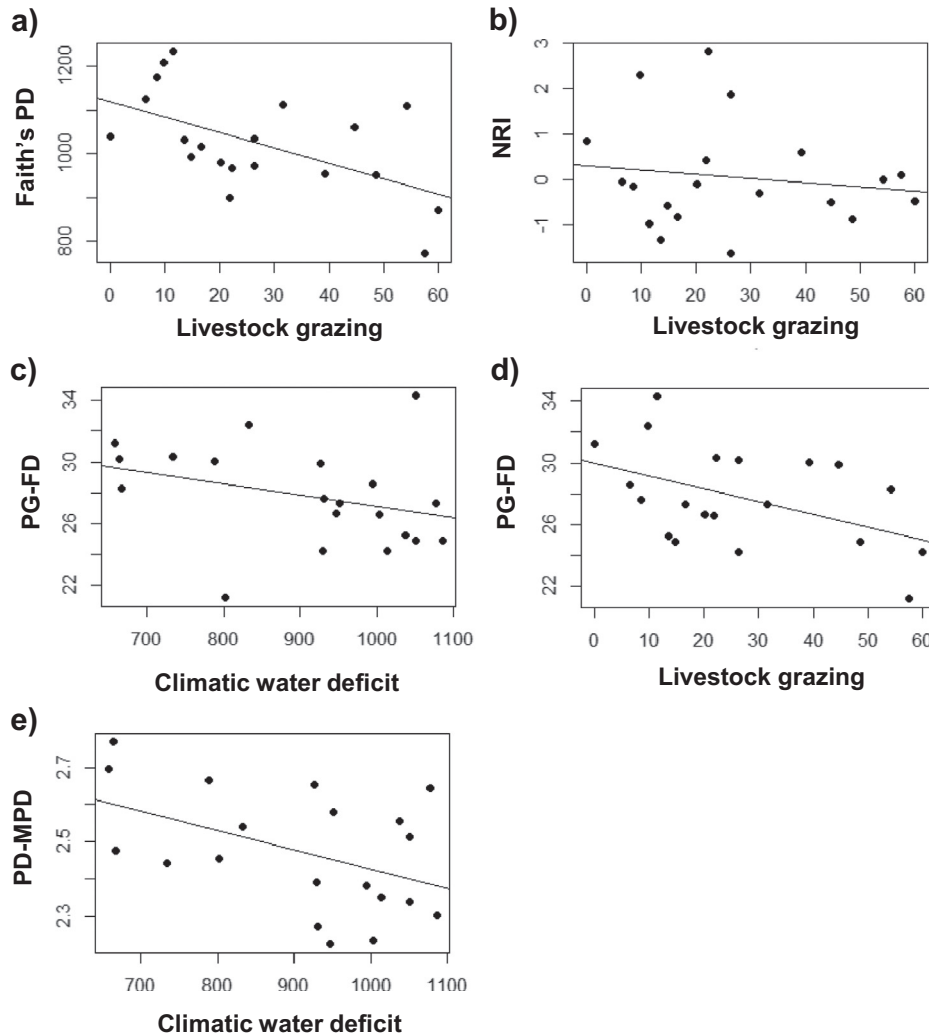
Table 3
Variables retained in the best-supported models analyzing how ant phylogenetic diversity and functional diversity change along aridity (climatic water deficit) and anthropogenic disturbance gradients in the Caatinga (Catimbau National Park, Pernambuco, NE Brazil). The positive and negative signs depict the direction of the relationship; an "X" signals that an interaction was present. The absence of any sign means there was no relationship between the response variable and the explanatory variable.

Response variable	Water deficit (WD)	Miscellaneous resource use (MU)	Livestock grazing (LG)	Wood extraction (WE)	MU × WD	Interactions LG × WD	WE × WD
Phylogenetic diversity							
PD			−				
MPD							
NRI	−	−	−		X		
MNTD							
NTI							
Functional diversity							
PG-FD	−		−				
FD-MPD	−						
FD-NRI							
FD-MNTD	−	−	−		X	X	
FD-NTI	+	+			X		

Fig. 2. Linear relationships between ant phylogenetic diversity and functional diversity metrics and the explanatory variables retained in the best-supported models: (a) Faith's PD and livestock grazing; (b) NRI and livestock grazing; (c) PG-FD and climatic water deficit; (d) PG-FD and livestock grazing; and (e) FD-MPD and climatic water deficit.

of evolutionary history shared by ants in the community (decrease in Faith's PD), but increased (although weekly) the non-random mean phylogenetic distance between ant species (decrease in the NRI). These results suggest that livestock grazing might act as an important filter, removing phylogenetically distant groups. Indeed, previous studies in the same area (Arcoverde et al., unpublished data; Oliveira et al., unpublished data) and in other Caatinga areas (Oliveira et al., 2017) found that populations of *Dinoponera quadriceps* (subfamily Ponerinae) decreased as disturbance increased. Alternatively, increased livestock grazing might non-randomly remove species from the most species-rich lineages or add species from relatively distant lineages (although not as distant as Ponerinae). Meanwhile, aridity and miscellaneous resource use appeared to have positive effects on phylogenetic diversity: as both pressures increased, the NRI decreased, which meant there was more phylogenetic overdispersion. Thus, these environmental gradients are important abiotic filters that may structure ant communities by removing species from different lineages in the most humid or least disturbed areas. Conversely, they may supply species from different lineages when disturbance or aridity increase. However, in the most arid areas, the NRI increased as disturbance increased, meaning that ant communities in areas experiencing high levels of both disturbance and aridity were more phylogenetically clustered. These results provide support for our second hypothesis—that disturbance and aridity can intensify each other's negative impacts on diversity. They also draw attention to the synergistic effects that anthropogenic disturbance and

climate change may have on biodiversity (Hirota et al., 2011; Ponce-Reyes et al., 2013; Gibb et al., 2015a; Frishkoff et al., 2016).

Disturbance and aridity play strong and consistent roles in reducing ant functional diversity, as evidenced by the functional responses that we observed along the disturbance and aridity gradients. Interestingly, these patterns cannot be explained by chance alone, since the effects were significant for the FD-NTI. Thus, aridity and certain forms of anthropogenic disturbance (i.e., livestock grazing and miscellaneous resource use) act as important abiotic filters of ant functional diversity in the Caatinga. More specifically, greater aridity and disturbance produced a major drop in the diversity of functions related to food acquisition and foraging habits. Interestingly, however, they did so in an interactive way. While miscellaneous resource use had very weak effects on FD-MNTD and the FD-NTI in the most arid areas of the park, its effects were quite strong in the less arid areas, which contradicts our second hypothesis. Given that functional diversity is already impoverished in highly arid areas, there might not be much room for further loss. In the less arid and more diverse areas of the park, however, disturbance can exert a much stronger influence. The effects of livestock grazing on FD-MNTD were also modulated by aridity: positive effects were found in the most arid areas, while negative effects were found in the least arid areas. Taken together, these findings present new evidence that anthropogenic disturbance and climate change, acting in tandem, can have complex effects on biodiversity (Travis, 2003; Ponce-Reyes et al., 2013; García-Valdés et al., 2015; Rito et al., 2017).
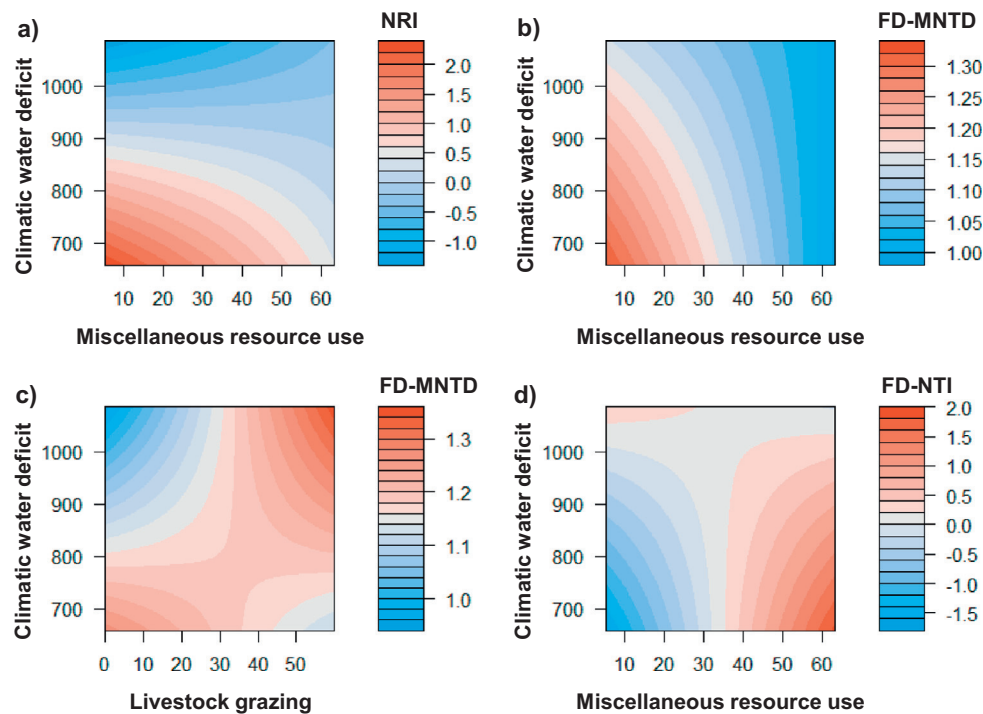
Fig. 3. Contour plots showing model results for the interactive effects of (a) climatic water deficit and miscellaneous resource use on the NRI; (b) climatic water deficit and miscellaneous resource use on FD-MNTD; (c) climatic water deficit and livestock grazing on FD-MNTD; and (d) climatic water deficit and miscellaneous resource use on the FD-NTI.

Our results do not match those of previous studies that analyzed the effects of aridity or precipitation (here, precipitation and water deficit were highly correlated: $r = 0.98$) on ant phylogenetic diversity and functional diversity. For instance, Arnan et al. (2015) examined geographical gradients in central and western Europe, Machac and collaborators (2011) examined three altitudinal gradients in the USA, and Smith (2015) examined several altitudinal gradients worldwide. All three found that mean precipitation had a weak to non-existent influence on ant phylogenetic diversity. Instead, patterns of phylogenetic diversity were primarily driven by mean temperature. In the case of functional diversity, no effects of mean precipitation were found along elevational gradients in northwestern Patagonia (Argentina) (Werenkraut et al., 2015) or across different vegetation types in the central North Kimberley region of Australia's seasonal tropics (Cross et al., 2016). In western and central European ant communities, functional diversity was found to be shaped by mean precipitation but was lowest in the wettest areas (Arnan et al., 2015). This pattern was attributed to relaxed local competition in areas with high levels of primary productivity and resource availability (Pavoine and Bonsall, 2011). Although mean precipitation does not generally seem to be an important driver of ant community structure at large spatial scales (Dunn et al., 2009; Andersen et al., 2015), our results suggest that water availability might significantly shape community structure in some regions or biomes, such as semi-arid areas where water is scarce (Parr et al., 2004).

In contrast, our discovery that disturbance reduced ant phylogenetic diversity and functional diversity corresponds to what has been found in many other studies (e.g., Bihn et al., 2010; Arnan et al., 2013, 2015; Liu et al., 2016). Interestingly, these studies explored the effects of acute disturbances—mainly land-use changes—which significantly drive down biodiversity (Sala et al., 2000). Other studies have also reported that intense grazing has negative effects on ant functional diversity in semi-arid areas (e.g., Chillo et al., 2017; Oliveira et al., 2017), but effects on invertebrate phylogenetic diversity have never before been reported. Our study is the first to highlight that small but constant biomass removal (i.e., chronic disturbance) can have similar deleterious effects on phylogenetic diversity and functional diversity as large, sudden biomass removal (i.e., acute disturbance). These findings are noteworthy given concerns about the functional consequences of current biodiversity losses (Bellard et al., 2012) that result from acute and chronic disturbances alike (Barlow et al., 2016).

We found strong phylogenetic signals in all the functional traits we measured (with the exception of relative clypeus length), indicating that more closely related ant species share more similar functional traits. These results agree with those of other studies that found significant and, frequently, strong phylogenetic signals in ant morphological traits (Machac et al., 2011; Donoso, 2014; Arnan et al., 2017). They also suggest that the functional morphological traits of ant species in the Caatinga are evolutionarily conserved, and consequently, a strong correlation between PD and FD patterns is to be expected (Webb et al., 2002; Cavender-Bares et al., 2009). However, we found that the phylogenetic diversity and functional diversity indices did not respond in the same way to disturbance and aridity gradients (Table 1). Other studies across very different taxonomic groups have observed similar mismatches, even when strong phylogenetic signals exist (e.g., Purschke et al., 2013 for plants; Devictor et al., 2010 for birds; Safi et al., 2011 for mammals; Arnan et al., 2015, 2017 and Liu et al., 2016 for ants). Our results thus lend further support to the idea that the environment may strongly condition covariation between different diversity components via differential filtering (Safi et al., 2011; Arnan et al., 2015, 2017).

From a conservation perspective, our results echo recent work demonstrating that CADs and aridity are immediate threats to biodiversity in SDTFs (e.g., Ribeiro et al., 2015, 2016; Ribeiro-Neto et al., 2016; Oliveira et al., 2017; Rito et al., 2017). However, this study is the first to describe these detrimental effects in an animal taxon in a species-rich SDTF such as the Caatinga. Ants provide a variety of key ecosystem services and disservices in most terrestrial ecosystems (Del Del Toro et al., 2012); these services are largely related to species dietary ecology. It is thus likely that a decline in both ant phylogenetic diversity and functional diversity (but especially in the latter) could have downstream effects on ecosystem processes, plant populations, and non-ant insect populations.

5. Conclusions

We need a clear understanding of the main factors threatening biodiversity in SDTFs. Conducted in Catimbau National Park, our study provides evidence that ant phylogenetic diversity and functional diversity can be deterministically impoverished due to increased anthropogenic disturbance and aridity, even if absolute levels of ant species diversity remain unchanged. More alarmingly, aridity can intensify the negative effects of disturbance. Taken together, our results underscore concerns about what will happen under future global change scenarios in neotropical semi-arid regions. These regions are already facing major declines in precipitation and constant-to-increasing anthropogenic exploitation of forest resources (Magrin et al., 2014). However, we observed that anthropogenic disturbance had most negative impacts in the wettest areas, which contain the highest levels of phylogenetic diversity and functional diversity. Caatinga conservation policies must thus give special priority to the wettest areas, where biodiversity loss could be the highest. Finally, our findings strongly suggest that studies in the Caatinga must address functional and phylogenetic diversity in addition to species richness if they wish to uncover how ant communities are reorganized after disturbance and how climate change modulates this process.

Acknowledgments

Appendices 1-6. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.03.037.

References

Andersen, A.N., Del Toro, I., Parr, C.L., 2015. Savanna ant species richness is maintained along a bioclimatic gradient of increasing latitude and decreasing rainfall in northern Australia. J. Biogeogr. 42, 2313–2322.

Anderson-Teixeira, K.J., Miller, A.D., Mohan, J.E., Hudiburg, T.W., Duval, B.D., DeLucia, E.H., 2013. Altered dynamics of forest recovery under a changing climate. Glob. Chang. Biol. 19, 2001–2021.

Arnan, X., Cerdá, X., Rodrigo, A., Retana, J., 2013. Response of ant functional composition to fire. Ecography 36, 1182–1192.

Arnan, X., Cerdá, X., Retana, J., 2015. Partitioning the impact of environment and spatial structure on alpha and beta components of taxonomic, functional, and phylogenetic diversity in European ants. PeerJ 3, e1241.

Arnan, X., Cerdá, X., Retana, J., 2017. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. Ecography 40, 448–457.

Baccaro, F.B., Feitosa, R.M., Fernández, F., Fernandes, I.O., Izzo, T.J., Souza, J.L.P., Solar, R., 2015. Guia para os gêneros de formigas do Brasil. INPA, Manaus, Brasil.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Mac Nally, R., et al., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 35, 144–147.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377.

Bihn, J.H., Gebauer, G., Brandl, R., 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. Ecology 91, 782–792.

Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., Ferrier, S., 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proc. Natl. Acad. Sci. U. S. A. 110, 9374–9379.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer-Verlag, New York.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. Ecol. Lett. 12, 693–715.

Chillo, V., Ojeda, R.A., Capmourteres, V., Anand, M., 2017. Functional diversity loss with increasing livestock grazing intensity in drylands: the mechanisms and their consequences depend on the taxa. J. Appl. Ecol. 54, 986–996.

Cross, A.T., Myers, C., Mitchell, C.N.A., Cross, S.L., Jackson, C., Waina, R., et al., 2016. Ant biodiversity and its environmental predictors in the North Kimberley region of Australia's seasonal tropics. Biodivers. Conserv. 24, 1727–1759.

Davidson, D.W., Cook, S.C., Snelling, R.R., 2004. Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. Oecologia 139, 255–266.

Del Toro, I., Ribbons, R.R., Pelini, S.L., 2012. The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecol. News 17, 133–146.

Development Core Team, R., 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Austria. URL, Vienna https://www.R-project.org/.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecol. Lett. 13, 1030–1040.

Dirzo, R., Young, H.S., Mooney, H.A., Ceballos, G., 2011. Seasonally Dry Tropical Forests. Ecology and Conservation. Island Press.

Donoso, D.A., 2014. Assembly mechanisms shaping tropical litter ant communities. Ecography 37, 490–499.

Dunn, R.R., Agosti, D., Andersen, A.N., Arnan, X., Bruhl, C.A., Cerdá, X., et al., 2009. Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. Ecol. Lett. 12, 324–333.

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61, 1–10.

Forest, F., Grenyer, R., Rouget, M., Davies, J., Cowling, R.M., Faith, D.P., et al., 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445, 757–760.

Frishkoff, L.O., Karp, D.S., Flanders, J.R., Zook, J., Hadly, E.A., Daily, G.C., et al., 2016. Climate change and habitat conversion favour the same species. Ecol. Lett. 19, 1081–1090.

García-Valdés, R., Svenning, J.C., Zavala, M.A., Purves, D.W., Araújo, M.B., 2015. Evaluating the combined effects of climate and land-use change on tree species distributions. J. Appl. Ecol. 52, 902–912.

Gibb, H., Sanders, N.J., Dunn, R.R., Photakis, M., Andersen, A.N., Angulo, E., et al., 2015a. Climate regulates the effects of anthropogenic disturbance on ant assemblage structure. Proc. R. Soc. Lond. B Biol. Sci. 282, 20150418.

Gibb, H., Stoklosa, J., Warton, D., Brown, A., Andrew, N., Cunningham, S., 2015b. Does morphology predict trophic position and habitat use of ant species and assemblages? Oecologia 177, 519–531.

Hirota, M., Holmgren, M., Van Nes, E.H., Scheffer, M., 2011. Global resilience of tropical forest and savanna to critical transitions. Science 334, 232–235.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Springer-Verlag, Berlin-Heidelberg, Germany.

Kaspari, M., Weiser, M., 1999. The size-grain hypothesis and interspecific scaling in ants. Funct. Ecol. 13, 530–538.

Klingenberg, C., Brandão, C.R.F., 2009. Revision of the fungus-growing ant genera Mycetophylax Emery and Paramycetophylax Kusnezov rev. stat., and description of Kalathomyrmex n. gen (formicidae: Myrmicinae: Attini). Zootaxa 2052, 1–31.

Leal, I.R., Tabarelli, M., Silva, J.M.C., Larcher, T.E., 2005. Changing the course of biodiversity conservation in the Caatinga of northeastern Brazil. Conserv. Biol. 19, 701–706.

Liu, C., Guénard, B., Blanchard, B., Peng, Y.-Q., Economo, E.P., 2016. Reorganization of taxonomic, functional, and phylogenetic ant biodiversity after conversion to rubber plantation. Ecol. Monogr. 86, 215–227.

Lutz, J.A., Van Wagtendonk, J.W., Franklin, J.F., 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. J. Biogeogr. 37, 936–950.

Machac, A., Janda, M., Dunn, R.R., Sanders, N.J., 2011. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. Ecography 34, 364–371.

Magrin, G.O., Marengo, J.A., Boulanger, J.P., Buckeridge, M.S., Castellanos, E., Poveda, G., Vicuña, S., 2014. Central and South America. In: Boulanger, J.P., Buckeridge, M.S., Castellanos, E., Poveda, G., Scarano, F.R., Vicuña, S. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., et al., 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33, 491–505.

Moreau, C.S., Bell, C.D., 2013. Testing the museum versus cradle biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. Evolution 67, 2240–2257.

Morlon, H., Schwilk, D.W., Bryant, J.A., Marquet, P.A., Rebelo, A.G., Tauss, C., et al., 2011. Spatial patterns of phylogenetic diversity. Ecol. Lett. 14, 141–149.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177.

Oliveira, A.P.C., Bernard, E., 2017. The financial needs vs. the realities of in situ conservation: an analysis of federal funding for protected areas in Brazil's Caatinga. Biotropica 49, 745–752.

Oliveira, F.M.P., Ribeiro-Neto, J.D., Andersen, A.N., Leal, I.R., 2017. Chronic anthropogenic disturbance as secondary driver of ant community structure: interactions with soil type in Brazilian Caatinga. Environ. Conserv. 44, 115–123.

Overbeck, G.E., Vélez-Martin, E., Scarano, F.R., Lewinsohn, T.M., Fonseca, C.R., Meyer, S.T., et al., 2015. Conservation in Brazil needs to include non-forest ecosystems. Divers. Distrib. 21, 1455–1460.

Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature 401, 877–884.

Parr, C.L., Robertson, H.G., Biggs, H.C., Chown, S.L., 2004. Response of African savanna ants to long-term fire regimes. J. Appl. Ecol. 41, 630–642.

Parr, C.L., Dunn, R.R., Sanders, N.J., Weiser, M.D., Photakis, M., Fitzpatrick, M.C., et al., 2017. GLobal ants trait database (GLAD): a new database on the geography of ant traits (hymenoptera: Formicidae). Insect Conserv. Divers. 10, 5–20.

Pavoine, S., Bonsall, M.B., 2011. Measuring biodiversity to explain community assembly: a unified approach. Biol. Rev. 86, 792–812.

Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5, 402–411.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.

Ponce-Reyes, R., Nicholson, E., Baxter, P.W.J., Fuller, R.A., Possingham, H., 2013. Extinction risk in cloud forest fragments under climate change and habitat loss. Divers. Distrib. 19, 518–529.

Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalski, S., Durka, W., et al., 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. J. Ecol. 101, 857–866.

Revell, L.J., 2012. Phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3, 217–223.

Ribeiro, E.M.S., Arroyo-Rodríguez, V., Santos, B.A., Tabarelli, M., Leal, I.R., 2015. Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. J. Appl. Ecol. 52, 611–620.

Ribeiro, E.M.S., Santos, B.A., Arroyo-Rodríguez, V., Tabarelli, M., Souza, G., Leal, I.R., 2016. Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. Ecology 97, 1583–1592.

Ribeiro-Neto, J.D., Arnan, X., Tabarelli, M., Leal, I.R., 2016. Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. Biodivers. Conserv. 25, 943–956.

Rito, K.F., Arroy-Rodríguez, V., Queiroz, R.T., Leal, I.R., Tabarelli, M., 2017. Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. J. Ecol. 105, 828–838.

Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armour-Marshall, K., Diniz-Filho, J.A.F., 2011. Understanding global patterns of mammalian functional and phylogenetic diversity. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 366, 2536–2544.

Sagar, R., Raghubanshi, A.S., Singh, J.S., 2003. Tree species composition, dispersion and diversity along a disturbance gradient in a dry tropical forest region of India. For. Ecol. Manag. 186, 61–71.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., et al., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Salas-López, A., 2017. Predicting resource use in ant species and entire communities by studying their morphological traits: influence of habitat and subfamily. Ecol. Indic. 78, 183–191.

Seddon, A.W.R., Macias-Fauria, M., Long, P.R., Benz, D., Willis, K.J., 2016. Sensitivity of global terrestrial ecosystems to climate variability. Nature 531, 229–232.

Singh, S.P., 1998. Chronic disturbance, a principal cause of environmental degradation 702 in developing countries. Environ. Conserv. 25, 1–2.

Smith, M.A., 2015. Ants, elevation, phylogenetic diversity and community structure. Ecosphere 6, 221.

Sociedade Nordestina de Ecologia, 2002. Projeto Técnico para a Criação do Parque Nacional do Catimbau/PE. Secretaria de Ciência. Tecnologia e Meio Ambiente de Pernambuco – SECTMA, Recife.

Swenson, N., 2014. Functional and Phylogenetic Ecology in R. Springer, New York.

Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc. R. Soc. Lond. B Biol. Sci. 270 (711), 467–473.

Ward, P.S., Brady, S.G., Fisher, B.L., Schultz, T.R., 2015. The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). Syst. Entomol. 40, 61–81.

Webb, C.O., David, D., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Evol. Syst. 33, 475–505.

Weiser, M.D., Kaspari, M., 2006. Ecological morphospace of new world ants. Ecol. Entomol. 31, 131–142.

Werenkraut, V., Fergnani, P.N., Ruggiero, A., 2015. Ants at the edge: a sharp forest-steppe boundary influences the taxonomic and functional organization of ant species assemblages along elevational gradients in northwestern Patagonia (Argentina). Biodivers. Conserv. 24, 287–308.